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STRUCTURE AND FUNCTION IN THE DEVELOPMENT OF SOME OF THE SPECIAL SENSES IN MAMMALS.

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H. H. Lane.

PREFACE.

The following paper was read before the Sigma Xi Club of the University of Oklahoma on the evening of December 13, 1915. It is to be regarded as a resume or preliminary report on a considerable amount of work on the correlation between structure and function in the development of the special senses in mammals done partly at the University of Oklahoma and partly at Princeton University. Acknowledgment is made of much encouragement and assistance on the part of Professor E. G. Conklin, Professor C. F. W. McClure, and Doctor Stewart Paton, all of Princeton University, Professor L. W. Cole of the University of Colorado, and to the National Academy of Sciences for a grant of $500.00 for the purchase of equipment necessary to continue the work and broaden its scope in a comparative way. The occasion and manner of its presentation will explain the form in which it is here presented. The full account of the whole investigation will be published elsewhere.

Possibly it may seem to some of you that your speaker owes you somewhat of an apology for asking your time and attention to this subject of structure and function in the development of the special senses. Watson, of Johns Hopkins University, in a recent book on "Behavior" (p. 49) asserts that: "Studies upon the structure of sense organs and upon the nervous system generally seem to be somewhat out of fashion at present," though he is kind enough to add (p. 50) that: "This condition of affairs is probably purely temporary," and outlines a "group of problems" (p. 31) in this field as follows: "The vast majority of the problems in both human and animal behavior may be grouped under one or another of three divisions: **I. Sense organ functions. II. Instinctive functions. III. Habit formation.** In addition to these large divisions in which the subjects for research lie, there remains the work of **IV. Correlation:** first, among behavior data—giving both an ontogeny and a phylogeny of behavior; second, of behavior with structure;

and finally the correlation of behavior and structure with physico-chemical processes."

An examination of Watson's volume as well as his previous work, not to mention that of other investigators in his field, reveals the fact that he refers only to the behavior of animals **after birth.** Some time before the statements quoted were written, or at least had appeared in print, I had undertaken a study of animal behavior from still another point of view, namely, the **prenatal** behavior of mammals and its correlation in ontogeny with the development of the structures concerned. Aside from some unpublished work of Paton on the guinea-pig, no work of this kind on mammals is known to me. Paton had in 1907 published in a Naples report an account of some related investigations on lower vertebrates and later two or three brief papers on the chick. Coghill, of Kansas University, and Herrick, of the University of Chicago, have obtained some very interesting and important results from a study of the swimming reflex in salamander larvae. A French investigator, Wintrebert, had previously, in 1904 and 1905, published some brief notes on some investigations which he had made on the axolotl and frog tadpole. With these exceptions, which, as you may readily see, are not exactly in line with studies about to be reported to you, the field of what, for want of a more exact term, may be called **prenatal behavior** has been practically untouched. A full account of the experiments and observations made to date will be published elsewhere, and would in their entirety be altogether too much to attempt to give in an hour's address, hence only a resume is contemplated here. Moreover, the problem is completed in only its broadest outlines and there yet remains much to be done to fill in the details. The program set for the future will require years of labor to bring to a successful conclusion, and will probably demand the attention of many additional investigators before its riches shall have been exhausted. The greater part of the investigation carried on for the past two years or so has been limited purposely to a study of one form, the albino variety of the Norway rat (Mus norvegicus albinus); but thanks to a generous grant from the National Academy of Sciences it is now possible to extend the range of the investigation over a number of species, in short, to make the study a comparative one, as should be done with all biological problems of this general nature.

In general terms the problem may be stated as follows: by

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means of suitable physiological experiments to determine just when the embryo first becomes possessed of the functions of touch, equilibrium, smell, taste, hearing, and sight; in other words, when it is first capable of receiving sensations of those sorts, and to determine furthermore the nature of the responses it is able to make at different stages in its ontogenetic development and to correlate its functional development with the structural development of the corresponding organs, namely, the central and peripheral nervous system, including organs of special sense.

Regarding the correlative relationship of structure and function, two views have chiefly demanded consideration at the hands of biologists. The first of these regards structure as the cause, or at least as the forerunner of function; while the second reverses the situation and regards function as the cause of structure. Some, like Conklin, have sought to develop an intermediate position, and regard neither as the cause of the other, but both as inherent properties of the organization fundamental to living matter. The view most commonly held regarding the origin of organs of special sense, either explicitly or implied, is that of the Lamarckian school of biology, namely, that they arose in phylogeny, at least, as adaptations to conditions of the external environment. Light, for example, impinging upon the surface of an organism led first to the deposition of pigment on the exposed part, and this ultimately became connected with the nervous system, and developed under the influence of continued use into a special light-perceiving organ. The Darwinians, of course, would modify the last statement by saying that in cases where the pigment spot happened to be connected with the nervous system, natural selection preserved it, and developed it into an organ of special sense.

If this has been the phylogenetic history of the eye, for example, it would be natural to expect that in ontogeny there would be some hint at this course of development, though it is now a well recognized fact that the recapitulation of phylogeny in ontogeny is never very exact, and often is obscured or entirely obliterated. But to find a course of development of even one organ of special sense exactly the reverse of that demanded by current theories should make us pause, and if a whole series of sense organs should give concurrent testimony adverse to the generally accepted theory, it would appear that a revision of that theory is urgently demanded.

With this idea in mind, let us examine some data from my work on the rat:

I. TOUCH:

The tactile sense is not only the most primitive but it is still the least differentiated of the special senses, so that it presents the logical point of first attack upon this problem. Of the fifteen stages of the rat examined, the youngest had a length (neck-rump) of only 7½ mm., and gave no evidence of the possession of a sense of touch. Stimulation with a fine sable brush, or with the prick of a fine-pointed needle brought about no perceptible response. The inductorium produced a change in the rate of the heart beat, but otherwise was no more effective than were the mechanical stimuli just mentioned.

When sectioned it was found that a large number of correlation or coordination fibers were already present in the spinal cord and brain stem. Both the afferent and efferent roots of the spinal nerves were present, although the former did not reach the integument. In the region of the snout two branches of the trigeminal nerve could be seen which however ended within the mesenchyme, i. e., did not reach the integument of that region. The vibrissae or "tactile whiskers" so prominent later in the life of the rat had not apparently begun to be formed; at any rate their anlagen could not be found.

The next stage obtained had an average length of 16 mm. and will therefore be referred to as the 16 mm. stage. By this time the tactile sense is present on theflanks and snout as evidenced by motor responses to the prick of the needle, though the more delicate stimulus of the sable brush was still ineffective. In the former case the response consisted of a turning movement of the head as a whole, and of slight but readily perceptible movements of the body when the stimulus was applied to the flank. There was at this time no sign as yet of the histogenesis of muscle in the snout region, and the turning movements of the head were so promptly made that there can be no question but that the stimulus was transmitted along nerve paths and not through the general protoplasm. Furthermore the sections demonstrate the presence of about a dozen anlagen of vibrissae on each side of the snout. These are innervated by branches of the maxillary division of the Vth, or trigeminal nerve, which ends in basket-like reticula in the vibrissal follicles.

In embryos 23 to 28 mm. long, stimulation with the sable brush produced reaction, as did also, of course, the needle-

prick. Again it was found that the snout region is most sensitive, though by this time stimulation with the needle about the shoulder, upper arm, hip, rump, and thigh also evoked motor responses. The sections show a noticeable increase in the number of the vibrissal anlagen as well as greater complexity in the neurofibral "basket" in each vibrissal follicle. The number of trigeminal fibers going to a single follicle has greatly increased since the 16 mm. stage. The general integument of the snout has not, however, yet received the terminations of other branches of the trigeminus, although many such are extending toward it, for the most part paralleling blood vessels in their course. In the 26 to 28 mm. embryos there are also correlation or coordination paths running between the medulla and the mid-brain.

In the 3.5 cm. fetus and new-born rats the tactile sense was still better developed over practically the whole of the body, tail, and limbs. The snout was, however, the most sensitive as was shown by the response to stimulation with a single hair, while elsewhere it took the mass pressure of the brush to elicit a response. Pain, or at least discomfort, was shown in the 3.5 cm. fetus one hour after removal from the mother's uterus, by the emittance of squeaks when pricked with the needle. Structurally speaking, there is in these stages an increased number of vibrissae on the snout; the anlagen of the body-hairs are very numerous, and the integument contains a rich plexus of nerve-fibers extending, at least in the snout region, through the stratum germinativum into the stratum intermedium of the epidermis. There is a notable increase in the number of afferent fibers of the trigeminus distributed to the snout region. The central connections are better marked and more extensive than in the preceding stages. The fibrillar baskets in the vibrissal follicles are now elongated, felted cylinders, from the bases of which the neurofibers emerge in a relatively large bundle some distance distad to the base of the follicle itself.

Throughout the older stages examined there was in general no particular advance in tactile sensibility over that just described. There was, however, a continued superiority of the snout region over the rest of the surface in sensitiveness to tactile stimuli and the use of the vibrissae as "feelers" became more and more marked. The structural advance in the tactile apparatus during these later stages is confined to an increase in the perfection of the mechanism already described.

Generalizing from the data which have been put before you only in a greatly abbreviated form, the following may be stated as a summary of the results, both experimental and observational, on the tactile sense: From the physiological standpoint there is no evidence of any tactile sense in the snout region before the formation of receptors or end-organs in the form of a basket-like reticulum about the bases of the anlagen of the vibrissae. The sense of touch in the snout region becomes more and more acute as the number of the terminal sense organs increases upon the development of additional vibrissae and by the innervation of the integument generally, into which the fibers of the trigeminus ultimately penetrate and form an extensive plexus.

The motor reactions to tactile stimuli on the snout region are at first simple movements of the head away from the source of stimulation. As central connections become perfected longer and gradually more complex reflex arcs are established and the simpler motor reactions of the earlier stages are replaced by such complex responses as efforts at the removal of an irritating object by the use of the paws, and the appearance of pain sensations as indicated by squeaks of greater or less vigor. It is probable that connection with the cortex has been formed at or even before birth, though it has been impoossible to be sure of this by direct observations.

The order of appearance of the different parts concerned with the sense of touch is therefore as follows:

1. The formation of a primitive reflex arc through the simultaneous laying down of both the afferent and efferent nerves and their connections in the medulla and cord.

2. The formation of effectors, or motor end organs, upon the histogenesis of those muscles that bring about the movements noted.

3. The formation of connections with higher brain centers, and, lastly, the establishment of the function upon the development of the terminal organs of touch, primitively the "baskets" in the follicles of the vibrissae, and later the complicated plexus in the epidermis.

In short, the structural mechanism precedes, or in is working order before the establishment of functional activity, and the **last element of this mechanism to be formed is the exteroceptive end-organ.**

II. EQUILIBRIUM:

In no stage previous to the 3.5 cm. fetus was there any experimental evidence of the presence of a sense of equilibrium. In the 7½ mm. embryo there are no traces even of the semicircular canals; in the 16 mm. stage, the semi-circular canals are definitely formed, so far as their gross structure is concerned, and the ampullae are innervated by branches of the vestibular nerve. The region of the cristae acusticae is indicated merely by an elongation of the endothelial cells. In the 23 to 28 mm. embryos the differentiation of the cells of the cristae acusticae is proceeding, but the sensory and supporting elements are not yet distinguishable. A fiber tract from the same general region of the medulla in which the vestibular nerve ends runs dorsad into the cerebellum and may indicate the establishment of a connection with the center for equilibration in that part of the brain, but any actual connection between the two cannot be determined in these preparations.

As already mentioned, the 3.5 cm. fetus was the first stage observed to give an indication of the possession of a sense of equilibrium. One hour after removal from the uterus the young of this stage were able to maintain an upright position of head and body, and to regain this position when disturbed. When turned entirely over onto the dorsum, infrequent and feeble efforts were made to right themselves. In the case of new born rats, i. e., rats during the first day after birth, it was observed that they crawled awkwardly about, turned the head from side to side, and when turned over onto the dorsum, made awkward righting movements which sometimes succeeded.

The structural features of the 3.5 cm. fetus and the young rats less than 24 hours after birth are practically identical so far as the apparatus for equilibration is concerned. The semicircular canals are larger than in the earlier stages described, the cristae acusticae have the sensory and supporting cells clearly differentiated. The former are inclosed each in a "stockade" of nerve fibers, in such a way as to transmit any stimulus produced by a change in the position of the animal. The central connections of the vestibular nerve are well defined.

Throughout the later stages there was manifested a gradual perfecting of the sense of equilibrium, accompanied by a gradually increasing power of coordination of movements. These stages in fact witness, from the structural standpoint, the addition, through the establishment of various coordination tracts,

of other factors concerned in the final perfection of the power of equilibration, notably (1) muscle tonus, (2) the use of the vibrissae, and (3) sight.

In short, our experimental and structural data on the sense of equilibrium show that this sense is first apparent upon the completion of the proprioceptive end-organ concerned, viz., the sensory cells of the cristae acusticae in the ampullae of the semi-circular canals, though the power of equilibration is gradually perfected through correlated development in other parts, principally in the muscular system (tonus), the eyes, and the vibrissae. Here as in the case of the sense of touch the whole of the reflex arc is completed before the function is established, and the last link in the chain is the proprioceptive end-organ.

III. SMELL:

Smell and taste are two very difficult senses to determine, especially in the very young stages with which for the most part these experiments dealt. In the case of embryos from 7½ mm. to 28 mm. long, no practical means for testing the sense of smell was devised. However, it is reasonably certain that the sense is lacking, for the histological differentaition of the olfactory epithelium has not advanced sufficiently far to enable the sensory cells proper to be distinguished, though it is during these stages, especially the younger ones, that the olfactory apparatus as a whole is being gradually laid down, both as regards its central and its peripheral portions.

The 3.5 cm. fetus showed no absolutely certain response to olfactory stimuli, though structurally both the central and distal portions of the olfactory apparatus show appreciable development over the preceding stages. The sensory cells in the olfactory epithelium, however, are not apparently fully differentiated.

During the first day after birth young rats seemed to perceive odors as evidenced by turning the head and movements of the snout as though sniffing; the reaction time was long, 15 to 30 seconds. At this time structural conditions indicate that the olfactory epithelium contains a few cells at least which are apparently fully differentiated as sensory cells, while the central connections are better developed than before. In later stages there is, on the whole, a gradual perfecting of the olfactory sense from day to day, accompanying the correlated differentiation of the olfactory epithelium.

In the case of smell, then, as in those of touch and equili-

brium, there is the early establishment of the olfactory nerves and of the various (at least the chief) olfactory tracts in the brain previous to and independent of the differentiation of the peripheral organ of smell,—the sensory cells of the olfactory epithelium. In short, in a reflex arc involving the sense of smell, the exteroceptive organ is the last link to be established, i. e., to become functional.

IV. TASTE:

The 3.5 cm. fetus could swallow, but neither in them nor in any preceding stages was there obtained any evidence of an ability to distinguish between savors of different sorts. At no time previous to birth could taste-buds or other fully differentiated organs of taste be found. During the first day after birth experimental results on taste were very inconclusive; apparently anything of a liquid nature applied to the lips or mouth, especially if the temperature were less than about 37.5° C., produced a feeling of discomfort. Sugar-solution, however, was received with much less apparent objection than salt- or acid-solutions, but this may have been due merely to its lack of the irritating properties connected with the salt- or acid-solutions. No taste-buds are present at this time, and while there are plainly developing in the fungiform papillae organs which can be in later stages identified as organs of taste, they have not attained their definitive form and structure at this time and are certainly not yet functional.

Though it was exceedingly difficult to distinguish between mere annoyance or discomfort and a sense of taste, it was apparent, especially from the ninth day on into the later stages examined, that this sense was present and gradually being perfected. Structurally there was a concomitant differentiation until by the ninth day after birth the new type of taste organ in the fungiform papillae had apparently reached functional maturity, while on and around the single circumvallate papilla the ordinary taste-buds are plainly becoming differentiated, though it is doubtful whether they are actually functional until later The two nerves concerned with the taste apparatus, namely, the lingual branch of the trigeminus and the glossopharyngeus, and their central connections are completed long before birth and hence long before a sense of taste is present. In this case. then, as was also noted for touch, equilibrium, and smell, the reflex arc involving the apparatus for taste is not completed until the proper exteroceptive organs are fully developed; in other

words, here as elsewhere the organ of special sense is the last link forged in the chain of neurones making up the reflex arc under consideration.

V. HEARING:

Absolutely no response to sound was noted before the twelfth day after birth. From that date until the sixteenth or seventeenth day there is a gradual increase in the ability to perceive sound. Previous to the twelfth day the cochlear nerve had long been well developed and its central connections fully established, but while the exteroceptive organ for sound, the organ of Corti, had been undergoing a gradual development also, it had not reached that degree of differentiation necessary for the perception of sound. By the twelfth or thirteenth day, however, the organ of Corti is apparently fully differentiated throughout a considerable portion of its extent, namely, about the middle third of its length, though the lumen of the external auditory meatus is not fully open. The next few days witness the completion of differentiation in the organ of Corti, and the complete opening of the meatus, establishing the sense of hearing in its entirety. Thus the sense of hearing falls into line with the observations on the previous senses considered,—touch, equilibrium, smell, and taste, and the same order of events occurs, namely, the early establishment of the auditory or cochlear nerve and its central connections; the late development of the organ of Corti and its accessory apparatus; or in other words the appearance of the sense of hearing depends upon the completion of differentiation in the exteroceptive organ of the auditory reflex arc, the sensory cells of the organ of Corti.

VI. SIGHT:

Absolutely no response to light was obtained before the opening of the eyes on the sixteenth or seventeenth day. Before the twelfth day after birth the eye is undergoing the usual course of development. By this time the rods and cones are still only fairly well defined, but the accessory structures are less fully developed and the closed lids prevent the entrance of any but possibly the very brightest light. By the sixteenth or seventeenth day, varying somewhat in different cases, the lids are open and the function of sight is fully established. The optic nerve and its central connections are early formed, before birth in fact. The very late differentiation of the retinal elements and the accessory structures of the eye in general be-

fore the power of sight is possessed by the young rat bring this sense into line with the conditions noted for the other senses, and reveal the fact that sight is not possible until the whole apparatus is in working order, of which the last element to be perfected is the exteroceptive end-organ.

The course of development of these special senses and of the structures correlated with them as just outlined is not in accordance with theory or **a priori** expectation. Following the early differentiation of the neural tube, the central connections between the afferent and efferent nerves are established in the spinal cord, at least, and probably also in the medulla before or simultaneously with the appearance of such nerves, which very soon acquire their proper terminations. The motor mechanism is next completed, including both the histogenesis of the muscle tissue and the formation of the end-plates of the efferent nerve-fibers; then there probably ensues the establishment of the (associational) connections with the higher centers of the brain; and last of all the peripheral receptive organs reach functional capability. This completes the arc, and for the first time external stimuli are able to start a reaction that passes from receptor to the centers and thence out to the effector.

It will be readily perceived that this is not the order of development demanded by the Lamarckian theory. If structure were to appear in response to function, i. e., from the effects of extrinsic stimuli, the logical order would be: receptor, afferent nerve, central connections, efferent nerve, and finally effector. But the evidence presented above shows clearly that such is not the case, but rather the reverse. The conclusion therefore is inevitable that **intrinsic** forces are chiefly concerned in the production in ontogeny of the mechanism of these special senses and their effector connections; they are forces introduced into the organism by heredity, that is, they inhere in the organization of the germ-plasm. The whole process is the product of germinal organization, though doubtless it is plastic enough to allow for a considerable degree of adjustment to minor environmental changes.

This investigation may serve to emphasize one other noteworthy fact that has struck the attention of all who have studied organic interrelations in the ontogeny of vertebrates, namely, the early appearance of the peripheral nervous system. Before it is possible that distinctly nervous functions can be

present, or if possible, of any importance to the embryo, the chief nerve trunks are all laid down, together with most or all their important branches. For example, both the vestibular and cochlear nerves are well developed in the 23 mm. embryo of the rat, if not earlier, while it is absolutely impossible that the function of hearing can have been established. We have shown that in our experiments the very first indication of an ability to detect sound comes not earlier than the twelfth day after birth, yet here when not more than two-thirds of the prenatal life has been passed through, the nerve of hearing is fully developed. In the 16 mm. embryo the vibrissae have not yet pierced the epidermis of the snout and it is hardly conceivable that the fetus has need of a delicate sense of touch to maintain itself within the amniotic sac; yet the maxillaris and mandibularis branches of the trigeminus are well formed, certainly capable of functioning, and terminate in very large and complex exteroceptive organs in the vibrissal follicles. It cannot be argued that in these and in other cases not necessary to be cited now, the nerves both afferent and efferent, and the receptors and effectors develop in **response** to functional activities or even functional needs on the part of the fetus at this or any preceding stage in its existence. The facts as stated, however, demand an explanation, and so far as I am aware such an explanation has not heretofore been attempted along the lines about to be set forth.

Harrison, of Yale, and others have studied, experimentally, the earliest stages in the development of the peripheral nerves, and from their results, especially from the cultivation of tissues **in vitro**, some light, it seems to me, is shed upon this question. Harrison finds that all tissues exhibit a specificity in their tendency to undergo each its own peculiar type of histogenesis, into muscle, epithelial, nerve, or connective tissue-cells, as the case may be. This inherent tendency of embryonic cells reveals itself irrespective of the nature of the external medium, provided it be not detrimental to the welfare of the cells concerned. A neuroblast inevitably becomes a nerve-cell because of the organization handed down to it through all the cell-generations from oosperm to neuroblast. This but confirms the conclusions of Whitman, Wilson, Conklin, Lillie, and many others, that there is a prelocalization of organ-forming substances in the egg at or before fertilization. In other words, the nervous system develops by a process of **endogenesis** or

genesis from within, i. e., by immanent processes, and not by **epigenesis.**

Not only is this true of the nervous system in general, but even the fate of each neuroblast and its processes is likewise predetermined. Thus Harrison has shown in the case of the formation of the axone that the outgrowth takes place "without the application of any external physical force and * * * occurs even when the normal surroundings are radically modified. That the original direction taken by the outgrowing fiber is already determined for each cell before the outgrowth actually begins, so that when it does begin it is dependent upon forces acting from within, follows first from the fact that the nerve fibers within the embryo tend to grow out in a given direction even when quite different surroundings are substituted for the normal, and secondly, from the fact that the nerve fibers which grow into the clotted lymph, are there surrounded on all sides by an isotropic medium, which cannot conceivably be held to produce movement in a definite direction."

Put into other words, we may say that the various structures of an organism are represented in some way in the oosperm, and make their appearance not in direct response to the needs or activities of the embryo, but in anticipation of them, because of the inherited forces in the egg, which become localized as development proceeds. They are "racial or inherent adaptations which are not first called forth by the contingent stimulus to which they are the appropriate and useful response" (Conklin).

It would appear, then, that the early establishment of the peripheral connections of nerves receives its proximate explanation in certain well-known mechanical relations that exist only at an early stage in embryonic development. Assuming the truth of the neurone hypothesis, the question of how any certain nerve reaches unerringly its proper termination receives an easy answer, though no question in all neurology has perhaps been more warmly debated. According to Harrison's experiments each neurone sends out its axone in a predetermined manner and direction. This axone has the form of a protoplasmic process with a bulb at its distal end from which finger-like pseudopods are constantly reaching out in various directions. The free length of this process may be as much as a millimeter or a little more, sufficient at an early stage in embryonic development for it to extend from the center of origin to the

muscle-fiber or epithelium with which it ultimately connects. That this activity must take place early in embryonic life is explained by the fact that it is only in these stages that the neuroblasts of the neural tube lie within the specified distance, about a millimeter or less, from the parts they are destined to innervate. That is to say, within the distance through which free growth of a nerve process is possible. On the basis of adaptation and natural selection, it is clear that only those embryos which succeed thus early in establishing these connections have a chance to develop properly and so to survive. This early growth of the neuroblasts and their processes is clearly, from the standpoint of behavior, a stereotropic response, as Harrison has shown, and the actual connections of the fibers with the particular cells of the receptors or effectors is due in like manner to chemotaxis, as Harrison also indicates, for it is hardly possible on any other grounds to explain how it comes about that in a nerve-trunk containing both afferent and efferent fibers, the latter turn aside to terminate in connection with muscle-cells, while the former continue in their course to the epithelial sense-cells.

Harrison points out another fact clearly shown by the observations here recorded upon the rat, namely, that the neuroblasts, thus early establishing terminal connections are relatively few in number, but once the connection has been made they are able to grow in length whenever and wherever the growth and shifting of organs or parts go on around them. Thus later nerve processes growing out from neighboring neuroblasts, in relation to the greater functional needs of the embryo, or as other conditons afford them opportunity, find even devious courses already determined for them and do not go astray from the path to their own particular end-organs. In this way one can see clearly the explanation for the very devious courses of some nerves and can account for the complex distribution of such a nerve as the vagus as it wanders about among such a varied lot of organs distributed along so much of the antero-posterior axis of the head and trunk.

Norman, Oklahoma, December 11, 1915.